The Modification Process of Sika Deer Impact on Forest Vegetation by Artificial Grasslands

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Contents

1. General Introduction

Ungulates (e.g., deer) can profoundly alter the structure and composition of forest communities via both direct and indirect mechanisms (Rooney and Waller 2003). Selective ungulate herbivory leads to the dominance of unpalatable species and/or tolerance-trait species in communities, which have chemical defense mechanisms or regrowth capacity (Augustine and McNaughton 1998). For instance, through experimental manipulation of white-tailed deer (*Odocoileus virginianus*) density, Nuttle et al. (2014) demonstrated that higher deer densities caused increased fern domination in the understory, decreased seedling number and forb cover, and diminished angiosperm richness. On the other hand, it is also known that ungulate herbivory on individual plants mitigates interspecific competition among plants, leading to high species diversity (Nishizawa et al. 2016). Moreover, Vild et al. (2017) showed that ungulate herbivory significantly increased α-and γ-diversity, and which caused significant vegetation homogenization inside the game preserve, and which caused by massive enrichment with ruderal species. In the Arctic, higher reindeer (*Rangifer tarandus*) densities have been linked to decreased plant species richness in less productive sites and to increased species richness in more productive sites (Sundqvist et al. 2018).

Many studies have suggested that ungulate herbivory affects forest regeneration and that the impact of the deer is driven by various factors. Cretaz and Kelty (2002) revealed that dense fern (*Dennstaedtia punctilobula*) understories showed differential interference among species with seedling development after deer browsing was reduced. Uno et al. (2019) showed that deer browsing had a direct negative effect on seedling survival as well as the indirect positive effect of reducing bamboo (*Sasa senanensis*) coverage in a cool-temperate mixed forest on Hokkaido. Murata et al. (2009) reported much greater negative effects of *Sasa borealis* than of sika deer browsing on seedling emergence and survival in cool-temperate mixed forests in Kyushu. Akashi et al. (2011) demonstrated that percentage of browsed seedlings was positively correlated with deer abundance, and that it was affected by deer seedling species preference in *Abies sachalinensis* plantations in Hokkaido. In addition, Gill and Beardall (2001) showed that deer greatly contribute to the seed dispersion of many plant species, and that plants with small, hard seeds are most likely to survive digestion. Hence, the effects of ungulate herbivory occur at different hierarchical scales, ranging from individual plants to whole forest ecosystems.

Deer have expanded their range and have increased dramatically in abundance worldwide in recent decades. Their impact on natural ecosystems has been accordingly dramatic

(Côté et al. 2004). In Japan, the population size and range of sika deer (*Cervus nippon* Temminck) have been rapidly increasing in many regions since the 1970s, and the impact of their herbivory on forest vegetation has increased remarkably (Takatsuki 2009). Hence, sika deer population control has been conducted to decrease the damage on agricultural production and forest ecosystems. Sika deer are medium to large ungulates native to Southeast Asia, eastern China, and Japan (Kalb et al. 2018), and they have become problematic in many regions in which they were introduced as novelties or games species as they hybridize with or are aggressive toward native deer species (Germany and Austria; Pitra et al. 2005, New Zealand; Husheer et al. 2006, USA; Kalb et al. 2018). Husheer et al. (2006) suggested that because of their dietary advantage, introduced sika deer may have a greater potential to impede forest regeneration and competitively exclude larger deer species, particularly at low basal area sites in which impacts on tree regeneration are likely to be greatest.

Deer impact on forest vegetation is driven by various factors, such as deer density (Côté et al. 2004), individual species characteristics (Horsley et al. 2003), light conditions (Suzuki and Ito 2014), snow depth (Kiffner et al. 2008), and so on. Recently, landscape composition has attracted attention as an important factor that strongly affects the impact of deer herbivory on forest vegetation. However, there are limited and inconsistent studies that have evaluated the degree to which browser impact on vegetation is scale-dependent on variation in ungulate density and habitat composition (Royo et al. 2017). Some studies have shown that herbivory intensity on the forest understory becomes lower in fields with rich food, such as pastures near to forests, than in fields without rich food (Takada et al. 2002; Honda et al. 2008; Royo et al. 2017). On the other hand, some studies have demonstrated that food-rich habitats increase the deer impact on surrounding forest (Reimoser and Gossow 1996; Iijima and Nagaike 2017). Therefore, it is important to generalize the process of how artificial landscapes affect deer impact on forest vegetation in order to understand forest dynamics.

Among various food-rich habitats, I focused on artificial grasslands, such as pastures, because they can provide a large quantity of high-quality and digestible grasses for deer (Takatsuki 2001). Previous studies have reported that deer often forage grasses in artificial grasslands (Trdan and Vidrih 2008; Kamei et al. 2010; Iijima 2018). Moreover, it has been suggested that artificial grasslands increase the population growth rate (Iijima et al. 2013) and the carrying capacity of sika deer (Iijima and Ueno 2016). In Japan, the area of artificial grasslands increased from 1965 (139,800 ha) to 1994 (661,400 ha). Since then, it has been declining and reached its lowest point (603,400 ha) in 2016 (MIAC 2016). Although there is some debate due

to the complexity of distinguishing artificial grasslands from other landscape components (Matsuura 2016), previous studies have suggested that artificial grasslands currently occupy 1%–5% of Japan's total land area (Ogura 2006, Matsuura et al. 2012). At first glance, this figure seems very low, but, considering the strong influence of artificial grasslands on sika deer, its effects should not be ignored.

Hence, to clarify the processes that modify how sika deer impact forest vegetation as a result of artificial grasslands, I conducted the following set of studies:

1. I aimed to clarify how artificial grasslands around forests affect the deer density in the forests and their impact on forest vegetation while considering the plant species at spatially finer scales (Chapter 2). Specifically, I examined whether 1) the surrounding abundant alternative food (in this study, artificial grasslands) in forests increase deer density and 2) the high deer density causes the more serious impact on forest vegetation. This chapter is in press.
2. I aimed to clarify the effect of presence/absence of artificial grasslands on sika deer (*Cervus nippon*) impact on forest vegetation (Chapter 3). I compared the occurrence of debarking and the coverage of understory vegetation in two adjacent regions under similar deer densities with and without artificial grasslands in Yamanashi Prefecture, Japan. This chapter was published in Takarabe and Iijima (2019).
3. I aimed to clarify the effect of presence/absence of artificial grasslands on the seasonal food habits of sika deer (Chapter 4). I conducted a pellets analysis to evaluate the seasonal food habits of sika deer in two adjacent regions under similar deer densities with and without artificial grasslands in Yamanashi Prefecture, Japan.
4. The final chapter contains a general discussion regarding the effects of artificial grasslands on deer impact on forest vegetation in a cool-temperate forest (Chapter 5).

2. Abundant artificial grasslands around forests increase the deer impact on forest vegetation

2.1 Introduction

Forest dynamics can be affected by various factors such as pathogens, typhoons, and wildfire. Furthermore, deer impact on forest dynamics has been scrutinized because of the increase in the abundance of large ungulates, especially deer species, in recent years (Rooney 2001; Côté et al. 2004). Such impact of deer browsing on forest regeneration has been stronger than has ground fires and canopy gaps (Nuttle et al. 2013). Deer browsing decreases the number of palatable forbs (white-tailed deer, *Odocoileus virginianus*: Rooney 2009; sika deer, *Cervus nippon*: Inatomi et al. 2017; Otsu et al. 2017; 2019) and saplings (sika deer: Akashi et al. 2015; Iijima and Nagaike 2015a; Uno et al. 2019). Deer also debark trees (red deer, *Cervus elaphus*: Verheyden et al. 2006; Vospernik 2006; sika deer: Iijima and Nagaike 2017), which may enhance tree mortality (sika deer: Ando et al. 2006; Nagaike in press). Consequently, deer affect the species composition of a forest because of the disappearance of palatable species (Mysterud 2006); thus, unpalatable species dominate the forest understory (Horsleyet al. 2003; Royo and Carson 2006). Impact by deer species on forests can remain depending on their cumulative impact, even when deer abundance decreases (Tanentzap et al. 2012; Nuttle et al. 2014). Furthermore, forests' susceptibility to such impacts may vary with other environmental factors such as the light condition in the understory (Suzuki and Ito 2014), the snow depth (Kiffner et al. 2008), and plant species involved (Partl et al. 2002). Therefore, it is important to clarify conditions that affect forests' susceptibility to deer impact to understand forest dynamics.

To comprehend the impact of deer on forest vegetation, the landscape composition around forests should be considered (Putman 1996). Landscape composition alters distribution, home range size, and population density of large ungulates (Saïd and Servanty 2005; Millington et al. 2010; Morellet et al. 2011). Specifically, deer population density sometimes increases in forests nearby pasture and/or agricultural lands (Aulak and Babińska-Werka 1990; but also see Takada et al. 2002). Furthermore, landscape composition surrounding a forest may alter the intensity of deer impact on that forest (Takada et al. 2002; Honda et al. 2008; Royo et al. 2017; Takarabe and Iijima 2019). Interestingly, Takada et al. (2002) and Royo et al. (2017) found that the browsing impact was less near forage-rich habitat. On the other hand, Alverson et al. (1988) and Iijima (2018) suggest that forage-rich habitat intensifies the browsing impact. There is limited

and inconsistent empirical evidence testing whether browsing impact on vegetation is scale dependent on variation in ungulate densities and habitat composition (Royo et al. 2017). Hence, it is important to clarify the ecological process through which food-rich habitats affect deer impact on forest vegetation to generalize the effect of food-rich habitats. Specifically, it is necessary to evaluate the deer density in forests surrounded by various food-rich habitat and deer impact on vegetation simultaneously.

Among various food-rich habitats, I focused on artificial grasslands such as pastures because they provide a large quantity of high-quality and digestible grasses for deer. Previous studies have reported that deer graze grasses in artificial grasslands (Trdan and Vidrih 2008; Kamei et al. 2010; Iijima 2018). Iijima (2018) showed that, except in winter, the relative abundance of sika deer was highly concentrated in artificial grasslands and in mosaic landscapes of forests and artificial grasslands. Thus, artificial grasslands are important habitats for deer.

Deer impact intensity is also affected by plant species composition. As deer density increases, angiosperm coverage decreases and unpalatable species such as ferns increase (Horsley et al. 2003; Nuttle et al. 2014). Dwarf bamboo is a dominant forest floor species, especially in the northern part of Japan. One of the dwarf bamboo species, *Sasa nipponica* is considered to have high tolerance for grazing by deer because its aboveground parts have a short life span (Takatsuki 1983) and it has a unique growth pattern: 1) The energy flows into aboveground parts from the underground parts, causing rapid growth of current culms and leaves above the ground in spring to summer. 2) The above ground parts stop growing, and the energy returns to underground parts for storage in autumn. 3) Overwintering culms and leaves decrease with the growth of new culms and leaves (Akiyama et al. 1977). This growth pattern avoids the accumulation of damage by deer browsing. Ando et al. (2006) reported that deer kill canopy trees by debarking, which may promote the expansion of dwarf bamboo (*S. nipponica*). The probability of tree debarking differs significantly among tree species (Akashi and Nakashizuka 1999; Iijima and Nagaike 2017), although it is also affected by deer density (Iijima and Nagaike 2015b). Hence, plant species should be considered when evaluating the impact of deer on vegetation.

The objective of this present study was to clarify how artificial grasslands around forests affect the deer density in the forests and their impact on forest vegetation while considering the plant species at spatially finer scales. Specifically, I examined whether 1) the surrounding abundant alternative food (in this study, artificial grasslands) in forests increase deer density and 2) the high deer density causes the more serious impact on forest vegetation.

2.2 Methods

2.2.1 Study site

My research was conducted in the Yatsugatake region of Yamanashi and Nagano Prefectures, central Japan. The Yatsugatake region is characterized by the mosaic landscape of forests and artificial grasslands (Fig. 2.1). I evaluated the landscape composition of the Yatsugatake region on the basis of the Natural Environment Information geographic information system (http://gis.biodic.go.jp/webgis/sc-023.html, accessed 15 Oct 2018) provided by the Biodiversity Center of Japan. In the web site, the plant community type shapefile of whole Japan was made in 1999 and is provided in a polygon format. Although all Japan's plant community is being resurveyed, some areas, including my study site, are not completed. Although minor changes in landscape composition may have occurred after 1999, there were no reports of large-scale habitat modifications in my study site. I categorized the plant community types into forest, artificial grasslands, and others. Artificial grasslands included grasslands for cattle grazing and growing grasses for the food of livestock, golf fields, ski fields, and parks. Grasslands for cattle grazing and growing grasses for livestock food in this region-are mainly covered with Timothy (*Phleum pratense*) and white clover (*Trifolium repens*). I had no data about plant species composition of golf fields, ski fields, and parks. Some of these artificial grasslands are fenced to prevent deer from entering; however, it is confirmed that deer could access all grasslands and graze grasses (Kanoko Takarabe, unpublished data). I established 207 plots in mature forests in the Yatsugatake region (Fig. 2.1) in the summer of 2015. To select plot locations, I first piled up a grid of 1 km square cells in the Yatsugatake region and selected the cells where the forest area percentage was larger than 50%. Then, I chose three plots per cell. The locations of three plots in each cell were selected for their environment. The distance among the three plots were greater than 100 m. Sometimes a plot within a cell was nearer to plots in other cells than those in the same cell. Plots were selected on the basis that 1) the canopy was closed and 2) the density of standing trees were similar. Northwestern and southeastern corners of all my research plots were N35°36.0′ E138°23.2′ and N35°54.5′ E138°30.7′, respectively. Mean annual precipitation from 2011 to 2015 at Ooizumi meteorological station (N35°51.7′ E138°23.2′, 867 a.s.l.) was 1181.7 mm. Mean, minimum, and maximum temperatures at Ooizumi meteorological station in 2015 were 7.1°C, −10.3°C, and 34.6°C, respectively. The meteorological station at Ooizumi does not

collect snow data, but snow generally covers the region from December to March to a maximum depth of about 50 cm. This region is dominated by natural and artificial forests (gray polygons in Fig. 2.1), scattered artificial grasslands (black polygons in Fig. 2.1), and large crop fields (diagonal lines in Fig. 2.1). The area percentages of forests, artificial grasslands, and crop fields were 59.5%, 8.1%, and 19.0%, respectively. Most crop fields occurred in the northeastern part of my research site, and the forests and crop fields were divided by a major road. Natural forests were primarily deciduous trees such as *Quercus crispula,* but they also included evergreen tree species such as *Abies homolepis*. Artificial forests were composed of deciduous trees such as *Larix kaempferi* and evergreen trees such as *A. homolepis* and *A. veitchii*.

Sika deer (*Cervus nippon*) are widely distributed in this region, and their 2015 density in Yatsugatake region was estimated at 48.3 deer/km^2 using the model of Iijima et al. (2013). Sika deer are annually harvested by game hunting from November 15 to March 15 and by pest control all year round. Sika deer are polygamous and monotocous. Sika deer generally eat graminoids, forbs, crops (Yokoyama et al. 2000), woody plants (Asada and Ochiai 1996), dwarf bamboo, and tree bark (Yokoyama et al. 1996); however, they also eat unpalatable plants and fallen leaves during famines (Takahashi and Kaji 2001). The diet of sika deer is wider than that of red deer (Davidson and Fraser 1991). The abundance of sika deer has been reported to be increasing (Iijima and Ueno 2016), and they browse understory vegetation (Iijima and Nagaike 2015b) and naturally emerged vegetation (Iijima and Otsu 2018), although debarking trees by sika deer (Nagaike and Hayashi 2003) is problematic in Yamanashi Prefecture.

2.2.2 Field survey

In this study, each plot was rectangular and measured 3 × 30 m. I surveyed the number of pellet groups in each plot. A pellet group was defined as a group of pellets that could possibly be excreted by a deer singularly on the basis of the size and color of pellets. Ten 1 × 1 m quadrats were positioned at 2 m intervals spanning the 30 m length of the plot, and each quadrat was surveyed for coverage of understory vegetation, the maximum height of understory vegetation, and the dominant species. I defined the understory vegetation as any plant species with height smaller than 2 m. I found two dwarf bamboo species (i.e., *S. nipponica* and *Sasamorpha borealis*; Table S1) that were the dominant species in each quadrat. Understory coverage in each quadrat was evaluated in 10% units. The coverage value of 0 indicates no vegetation (0%), whereas that of 1 indicates full vegetation coverage (100%). Within each plot, I also measured the diameter at

breast height (DBH) of species and the occurrence of debarking and fraying (hereafter, I shall use the word “debarking” for both of debarking and fraying) by sika deer of all trees measured with a DBH of > 5 cm. I conducted all these surveys from August to October in 2015.

2.2.3 Statistical analysis

In this study, I hypothesized that abundant artificial grasslands around forests increase deer abundance in forests and the deer reduced the coverage of understory vegetation by browsing and increased the occurrence of debarking of standing trees (Fig. 2.2). As deer density increases, it has been shown that the coverage of angiosperms decreases (Horsley et al. 2003; Nuttle et al. 2014) and the probability of debarking of trees increases (Iijima and Nagaike 2015b). Hence, I used understory vegetation coverage and the presence/absence of debarking on trees as a deer impact index on understory vegetation and standing trees, respectively. Repeated deer browsing was expected to decrease understory vegetation coverage. Debarking trees occurs in winter and summer in some parts of Japan (Ando et al. 2004), and the scars of debarking are long-lasting. Although I evaluated the relative deer abundance by the number of pellet groups in summer and did not check when the debarking occurred because I surveyed the presence/absence of debarking only once, the coverage of understory vegetation and tree debarking are the cumulative indices as stated above. Hence, comparing pellet group numbers and these deer impact indices is justified. The factors for the variation of the pellet number group numbers were evaluated by the following the generalized linear model (GLM).

$$\mathrm{PG}_p \sim \mathrm{Poisson}\left(\exp\left(\alpha 1 + \beta_{\mathrm{GR}} \times \mathrm{GR}_p + \beta_{\mathrm{FT}} \times \mathrm{FT}_p + \beta_{\mathrm{SL}} \times \mathrm{SL}_p + \beta_{\mathrm{CR}} \times \mathrm{CR}_p\right)\right)$$

where PG_p is the number of pellet groups within each plot, $\alpha 1$ is the intercept, β_{GR} is the coefficient of the percentage of artificial grassland area within a circle buffer with various radiuses (GR_p) from the center of a plot, β_{FT} is the coefficient of the forest type of a plot (FT_p) that takes 1 if the major species of canopy trees are evergreen species or takes 0 otherwise, β_{SL} is the coefficient of the slope of a plot (SL_p), and β_{CR} is the coefficient of the percentage of crop field area within a circle buffer with various radiuses (CR_p) from the center of a plot. The radiuses of a circle of GR_p and CR_p were from 200 to 2000 m at 200 m intervals. I thought that the degree of artificial grasslands effects was mainly affected by the abundance (i.e., percentage within a circle buffer) of artificial grasslands and several large and small artificial grasslands are scattered on my study area (Fig. 2.1). Thus, I used the percentage of artificial grasslands in a circle buffer from the center of a forest plot instead of the distance from artificial grasslands to evaluate the effects of artificial

grasslands with various size. I attempted to incorporate spatial random effect as a Gaussian conditional autoregressive (CAR) model (Latimer et al. 2006) into the GLM. However, the distance between plots was not regular (Fig. 2.1), and it was impossible to define adjacent plots from certain plots, especially when a small radius buffer was mandatory to estimate the CAR model. Furthermore, there was one observation result per plot, so use of random effect might cause over-fitting. I incorporated FT_p for considering the effect of light condition on the coverage of understory vegetation. Because I carefully selected plots where 1) canopy was closed and 2) the density of standing trees was similar, the understory of evergreen forests is expected to be darker than that of deciduous forests.

The factors for the variation of the coverage of understory vegetation were evaluated by the following hierarchical Bayes model.

$$\mathrm{CO}_q \sim \mathrm{Beta}(\alpha_q, \beta_q)$$

$$\alpha_q = \mu_q \times \varphi$$

$$\beta_q = (1 - \mu_q) \times \varphi$$

$$\mu_q = \frac{1}{1 + \exp\left(-\left(\alpha 2 + \beta_{\mathrm{PG}} \times \mathrm{PG}_p + \beta_{\mathrm{FT2}} \times \mathrm{FT}_p + \beta_{\mathrm{VT}} \times \mathrm{VT}_q + \varepsilon_p\right)\right)}$$

where CO_q is the coverage of understory vegetation within a quadrat, $\alpha 2$ is the intercept, β_{PG} is the coefficient of the number of pellet groups within a plot (PG_p), β_{FT2} is the coefficient of the forest type of a plot (FT_p) that takes 1 if the major species of canopy trees is evergreen or takes 0 otherwise, β_{VT} is the coefficient of vegetation type of understory vegetation of a quadrat (VT_q) that takes 1 if the dominant species is *S. nipponica* or takes 0 otherwise, and ε_p is the random effect of each plot. I incorporated FT_p for considering the effect of light condition on the coverage of understory vegetation. Because I could not directly measure the light quantity, I used forest type alternatively. Because I carefully selected the plots with the criteria as 1) canopy was closed and 2) the density of standing trees was similar, it is expected that the light condition of the evergreen forest is darker than that of the other forest type. I also incorporated VT_p because *S. nipponica* is considered to have high tolerance for grazing by deer. Beta distribution can take values between 0 and 1, and the shape of beta distribution is determined by two parameters (usually denoted as α and β). The expected value of beta distribution (μ) is defined as $\alpha / (\alpha + \beta)$. I wished to examine the effects of factors that were explained as above on the expected value of coverage (i.e., μ). It is convenient to introduce a new parameter $\varphi = \alpha + \beta$ to parameterize α and β. By using φ, α can be expressed as $\mu \times \varphi$ and β can be expressed as $(1 - \mu) \times \varphi$. If the coverage was 0 or 1, I added the value 10^{-6} to 0 or subtracted the value 10^{-6} from 1, respectively. Prior

distributions of $\alpha 2$, β_{PG}, β_{FT2}, and β_{VT} were a Gaussian distribution, with a mean value of 0 and a variance of 1000. Prior distribution of ε_p was also a Gaussian distribution, with a mean value of 0 and a variance of σ_{CO}^2. Prior distribution of σ_{CO} is a vague uniform distribution, ranging from 0 to 100 (Gelman 2006). Prior distribution of φ was a vague uniform distribution, ranging from 0 to 1000.

I evaluated the factors for the occurrence of debarking on standing trees by the following hierarchical Bayes model.

$$\mathrm{DE}_i \sim \mathrm{Bernoulli}(pd_i)$$

$$pd_i = \frac{1}{1 + \exp\left(-\left(\alpha 3 + \beta_{PG2} \times \mathrm{PG}_p + \beta_{DBH} \times \mathrm{DBH}_i + \beta_{SL2} \times \mathrm{SL}_p + \beta_{SP,i} + \varepsilon 2_p\right)\right)}$$

where DE_i is the occurrence of debarking that takes 1 if an ith tree was debarked or takes 0 if the tree was not debarked, $\alpha 3$ is the intercept, β_{PG2} is the coefficient of the number of pellet groups within a plot (PG_p), β_{DBH} is the coefficient of diameter at breast height of an ith tree (DBH_i), β_{SL2} is the coefficient of SL_p, $\beta_{SP,i}$ is the coefficient of tree species of an ith tree, and $\varepsilon 2_p$ is the random effect of each plot. Prior distributions of $\alpha 3$, β_{PG2}, $\beta_{DBH,}$ and β_{SL2} were normal, with a mean value of 0 and a variance of 1000. Prior distributions of β_{SP} and $\varepsilon 2_p$ were a Gaussian distribution, with a mean value of 0 and variances σ_{SP}^2 and σ_{DE}^2. Then, the high or low coefficient of β_{SP} means the relative evaluation of deer palatability among tree species that are treated in this study. Prior distributions of σ_{SP} and σ_{DE} were a vague uniform distribution, ranging from 0 to 100. In the analysis of the occurrence of debarking on standing trees, I excluded tree species that numbered <10 in all plots.

The Bayesian information criterion (BIC; Aho et al. 2014) was used to determine the best buffer radius from the aspect of model fitting to data. Parameter estimation of the GLM was conducted by iteratively reweighted least squares method that was implemented in the *glm* function of R (R Core Team 2018). Estimation posterior distribution of hierarchical Bayes models were conducted by the Markov chain Monte Carlo (MCMC) method that was implemented by R (R Core Team, 2018), JAGS (Plummer 2003), and the package "rjags" (Plummer 2018) of R (R Core Team, 2018). I ran three parallel MCMC chains and retained 15,000 iterations after an initial burn-in of 15,000 iterations. I thinned the sampled values to approximately 6.7% (i.e., obtained 1000 samples as posterior distributions for each chain). MCMC sampling was considered to have converged when the "R hat" value became <1.1 (Gelman et al. 2004). A coefficient was confirmed to be significantly affected (in terms of the response variable) if the 95% credible intervals of that estimated coefficient did not overlap 0.

2.3 Results

The mean, minimum, and maximum of number pellet groups per plots were 5.329, 0, and 48, respectively. Among the models using a circle buffer of various radiuses (200 to 2000 m) from the center of a plot, the model using the circle buffer of 1000 m radius showed the minimum BIC value (Table 2.1). The pellet group number was significantly high in forests with the higher percentage of artificial grassland area, the lower percentage of crop field area, and in evergreen forests compared with that in other forest types (Fig. 2.3, Table 2.1), whereas it did not show a significant effect of the slope of plots.

I found 49 dominant plant species in all quadrats (Table S1), which primarily included *S. nipponica* that had a mean, minimum, and maximum height of 58.6, 15, and 111 cm, respectively. The understory vegetation coverage was significantly low in forests with many pellet group and in evergreen forests than in deciduous forests. *S. nipponica* had greater coverage than had other vegetation types (Fig. 2.4, Table 2.2).

I found 62 tree species in all plots (Table S2). The mean and standard error of standing tree density of a plot were 1123 ± 3.1 (/ha). The mean and standard error of the basal area (BA) of standing tree were 35.9 ± 0.1 (m^2/ha). The dominant species based on the aspects of tree density or BA in each plot were mostly *Larix kaempferi* and *Quercus crispula*. The mean, minimum, and maximum of the occurrence of debarking on standing trees per plots were 21%, 0%, and 100%, respectively. Small trees in DBH were more likely to be debarked, and the probability of occurrence of debarking was higher in a plot with many pellet groups (Fig. 2.5, Table 2.3). The occurrence probability of debarking differed among tree species; for *Fraxinus lanuginosa*, *Clethra barbinervis*, *Swida controversa*, and *Abies veitchii*, it was significantly high, whereas for *Malus toringo*, *Betula platyphylla*, *Pinus densiflora*, and *Betula davurica*, it was significantly low (Fig. 2.6).

2.4 Discussion

This study demonstrated that the abundant surrounding artificial grasslands increased deer density in forests, and which caused the more serious deer impact on forest vegetation. Artificial grasslands are expected to be attractive food resources, wherein deer often forage these grasses (Trdan and Vidrih 2008; Kamei et al. 2010; Iijima 2018), and larger artificial grassland proportions cause an increase in population growth (Iijima et al. 2013) and carrying capacity

(Iijima and Ueno 2016). Therefore, it is expected that the sika deer density is high in the forests where there are large artificial grasslands around them. In fact, regardless of buffer size, the number of pellet groups was high in forests with higher percentages of artificial grasslands (Table 2.1).

The number of pellet groups was significantly small in plots where crop field percentages were high (Table 2.1). These results are consistent with the study of Agetsuma et al. (2016), which showed that deer density was negatively affected by percentage of area covered by agricultural land. Crop fields provide food resources for deer; however, in my research area, artificial grasslands are surrounded by large forests, whereas crop fields were adjacent to fragmented forests. Therefore, it is expected that the crop fields were less approachable than artificial grasslands. Moreover, crop fields have relatively high levels of human activity. These combined factors may reduce deer density around crop fields.

The coverage of understory vegetation was significantly low in the plots where many pellet groups were found (Fig. 2.4, Table 2.2). Previous studies have also supported the strong impact on understory vegetation by a high deer density (Côté et al. 2004; Takatsuki 2009). In context of deer browsing, several studies have reported a reduction or disappearance of the coverage of understory vegetation (Nomiya et al. 2003; Rooney and Waller 2003; Szabo et al. 2004). However, the effect of deer browsing differs among understory species. For instance, *S. nipponica* is known to be have high tolerance-trait for grazing (Takatsuki 1983). In the present study, I found that *S. nipponica* had significantly greater coverage than had other species (Fig. 2.4, Table 2.2), which is supported by a previous study (Ando et al. 2006). Therefore, the type of understory vegetation must be considered while measuring the effect of browsing.

The occurrence of debarking on standing trees was significantly high in the plots where many pellet groups were found (Fig. 2.5, Table 2.3). Previous research has reported high debarking risk under a high deer density (Iijima and Nagaike 2015b). However, small trees in terms of DBH were significantly more debarked (Fig. 2.5, Table 2.3), and some species (*F. lanuginosa*, *C. barbinervis*, *S. controversa*, and *A. veitchii*) were preferentially debarked (Fig. 2.6). Therefore, small individuals or/and such palatable species may be debarked when deer density is not high (Figs. 5 and 6).

There is no consistent trend on how food-rich habitat affects browsing impact on forest vegetation (Putman and Staines 2004). Takada et al. (2002) found that plant species richness and plant coverage were significantly higher in sites adjacent to agricultural fields than in sites remote from agricultural fields. Royo et al. (2017) found that the impact of browsing weakened and

ultimately disappeared as the proportion of forage-rich habitats (e.g., recent harvests) increased. In contrast, the number of deer pellet groups was high in the plots with surrounding abundant artificial grasslands (Table 2.1) and the deer impact on forest vegetation was high in such plots (Figs. 4 and 5) in my study as stated above. What is the cause of the difference? Takada et al. (2002) detected no difference in the number of deer fecal pellets found in sites adjacent to and remote from agricultural fields. Furthermore, Royo et al. (2017) also assumed deer populations were relatively stable throughout the landscape in their study. However, my study showed that local densities of sika deer greatly differ depending on the surrounding landscape components even if the regional deer population density is stable. Therefore, the effect of food-rich habitat on forest vegetation may differ depending on the spatial scale. In conclusion, abundance food-rich habitat around forests increase deer density in forests that lead to higher impact on forest vegetation in spatially fine scale.

2.5 Figures

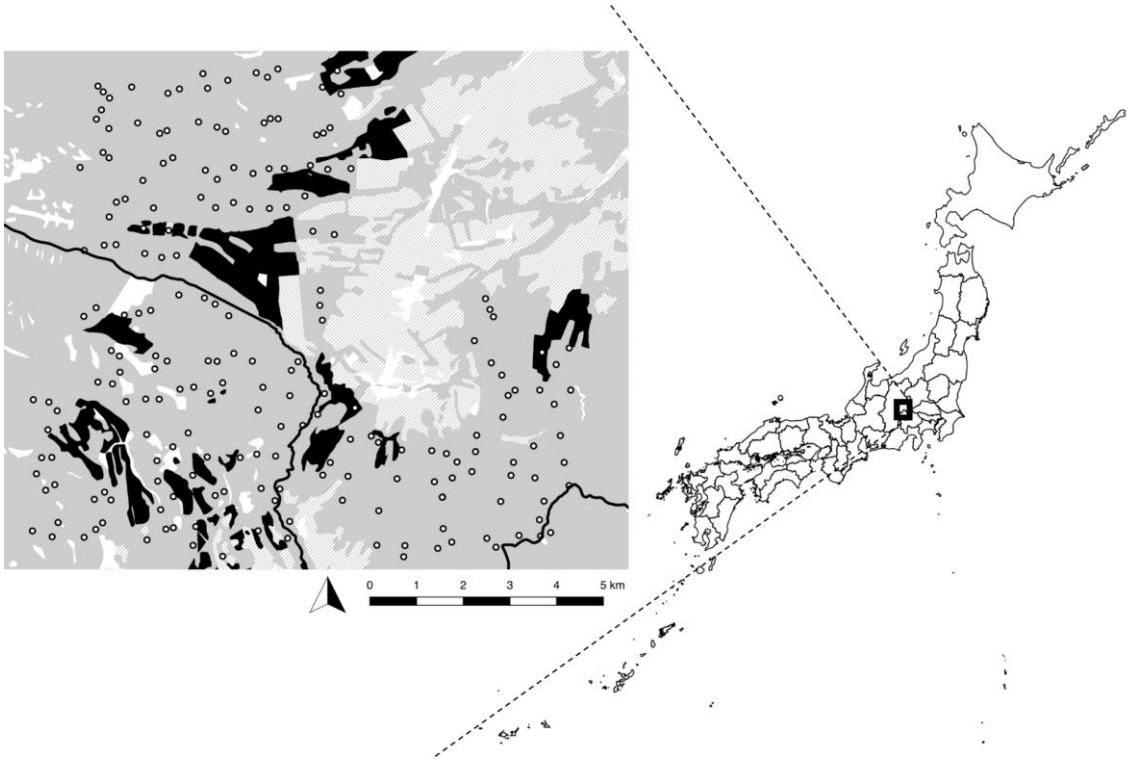

Fig. 2.1. Map of research site

Circles indicate each plot. Black and gray polygons indicate artificial grasslands and forests, respectively. Polygons with diagonal lines indicates crop fields. Solid black lines indicate the prefectural boundary.

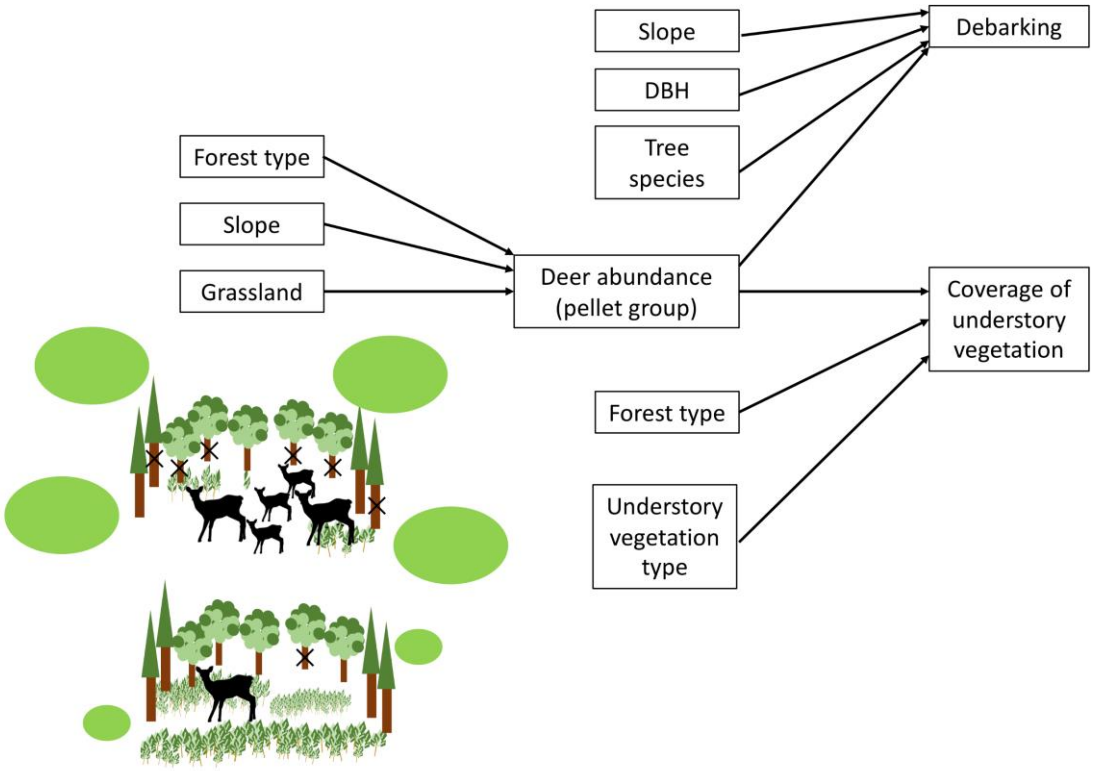

Fig. 2.2. Schematic diagram of the model structure

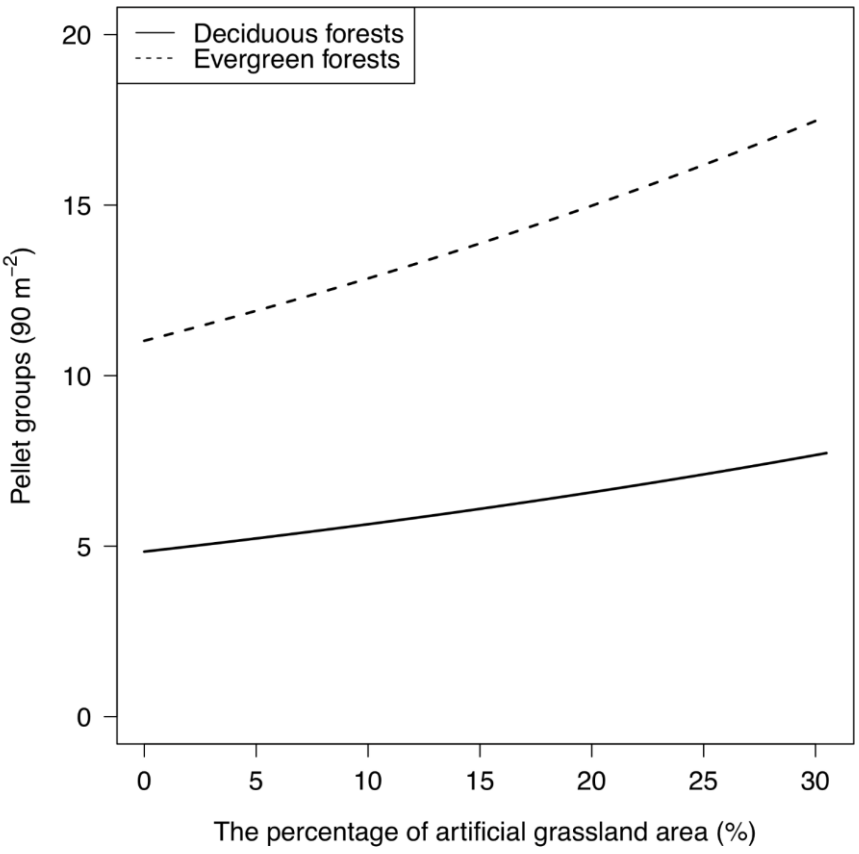

Fig. 2.3. Estimated number of pellet groups

Solid and dotted lines indicate the estimated number of pellet group in deciduous forests and evergreen forests, respectively.

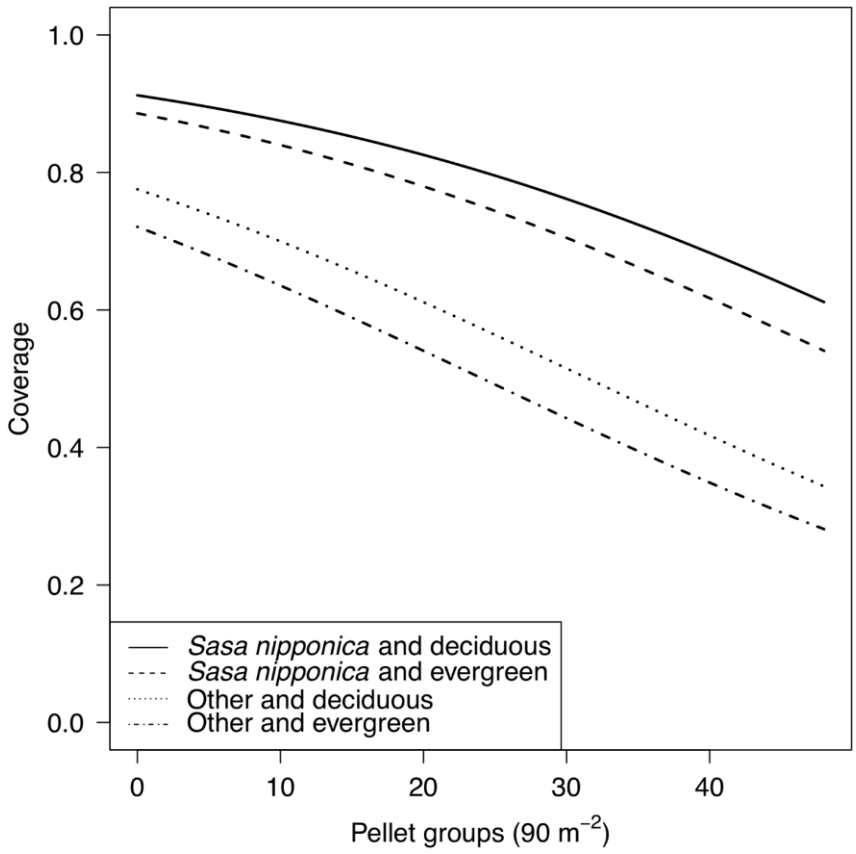

Fig. 2.4. Estimated coverage of understory vegetation

The coverage of understory vegetation was evaluated by 10 % units. The coverage value of 0 indicates no vegetation (0%) and that of 1 indicates full vegetation coverage (100%). Each line corresponds to the estimated coverage of understory vegetation that is affected by the number of pellet groups, the type of understory vegetation, and the forest type (whether the major tree species of canopy trees is evergreen or others).

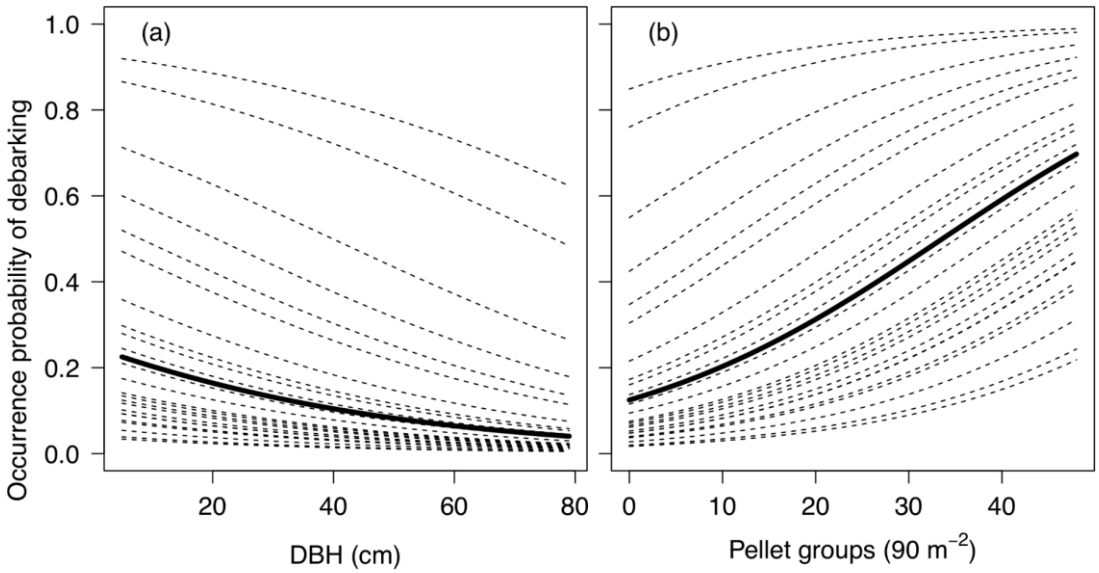

Fig. 2.5. Estimated probability of the occurrence of debarking

(a) Relationship between the probability and the diameter at breast height (DBH). (b) Relationship between the probability and the number of pellet groups. Each dotted line that indicates each tree species corresponds to either (DBH) and the number of pellet group for the occurrence probability of debarking. Solid line indicates the mean of them.

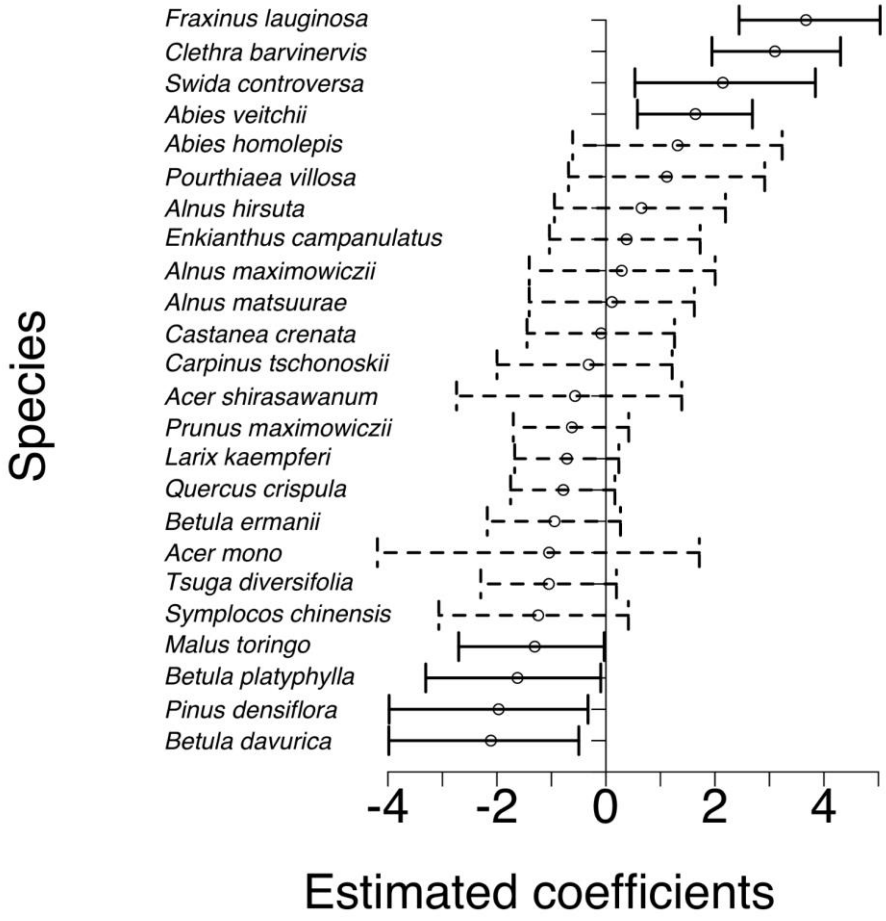

Fig. 2.6. Estimated coefficient of each tree species about the occurrence of debarking

The prior distribution of the coefficients of tree species was a Gaussian distribution with a mean value of 0. Circles and bars indicate the mean and 95 % credible intervals of estimated coefficients. Solid and dotted lines indicate statistically significance that was evaluated whether 95% credible intervals of that estimated coefficient did overlap 0 or not.

2.6 Tables

Table 2.1 The BIC and GLM coefficients about the number of pellet group with different buffer radius about the percentage of grassland area and crop field area

Buffer	Estimated coefficients					BIC	Percentage of artificial grassland area within a circle buffer (%)		
radius (m)	$\alpha 1$	β_{GR}	β_{FT}	β_{SL}	β_{CR}		Mean	Min	Max
200	1.505	0.356	0.953	-0.001	-6.298	2251.4	4.2	0.0	83.8
400	1.522	0.825	0.915	-0.001	-6.716	2204.6	5.6	0.0	65.6
600	1.572	0.861	0.877	-0.002	-6.229	2185.5	7.1	0.0	46.4
800	1.584	1.045	0.845	0.000	-6.784	2151.3	7.8	0.0	35.2
1000	1.577	1.535	0.823	0.001	-7.016	2125.5	8.1	0.0	30.5
1200	1.650	1.212	0.806	0.000	-6.475	2139.6	8.4	0.0	30.7
1400	1.671	0.994	0.800	0.000	-5.750	2157.8	8.6	0.0	31.3
1600	1.708	0.672	0.789	0.000	-4.962	2183.0	8.7	0.0	30.5
1800	1.740	0.404	0.781	-0.001	-4.327	2203.3	8.7	0.0	27.1
2000	1.734	0.465	0.775	-0.001	-4.043	2213.5	8.6	0.0	23.6

$\alpha 1$ is the intercept; β_{GR} is the coefficient for the percentage of grassland area; β_{FT} is the coefficient of forest type of a plot that take 1 if canopy trees of a plot is mainly dominated by evergreen species or take 0 otherwise; β_{SL} is the coefficient of the slope of a plot; β_{CR} is the coefficient for the percentage of crop field area. BIC is the Bayesian Information Criterion (Aho et al. 2014).

Table 2.2 Estimated coefficient of hierarchical Bayes model about the coverage of understory vegetation

Coefficient	Mean	SD	95 % Credible interval		Significance
			Lower	Upper	
α2	1.383	0.136	1.113	1.648	*
β_{FT}	-0.077	0.244	-0.555	0.398	
β_{PG}	-0.037	0.010	-0.056	-0.016	*
β_{VT}	0.929	0.124	0.684	1.175	*
σ_{CO}	1.164	0.070	1.035	1.310	-
φ	2.345	0.094	2.166	2.531	-

α2 is the intercept; β_{FT}, the coefficient of forest type that take 1 if canopy trees of a plot is mainly dominated by evergreen species or take 0 otherwise; β_{PG}, the coefficient of the number of pellet group within a plot; β_{VT}, the coefficient of vegetation type of understory vegetation of a quadrat (it takes 1 if the dominant species is *Sasa nipponica* or takes 0 otherwise); σ_{CO}, a standard deviation parameter of ε_p that is the random effect of each plot; φ, a derived parameter as the sum of two parameters of beta distribution (i.e., α and β). If the 95% credible intervals of that estimated coefficient did not overlap 0, the factor was evaluated statistically significant. "-" in "Significance" column indicates the meaninglessness of significance because σ_{CO} and φ cannot take negative values.

Table 2.3 Estimated coefficient of hierarchical Bayes model about the occurrence of debarking on standing trees

Coefficient	Mean	SD	95 % Credible interval		Significance
			Lower	Upper	
α_3	-1.479	0.546	-2.544	-0.384	*
β_{DBH}	-0.026	0.011	-0.049	-0.004	*
β_{PG2}	0.058	0.020	0.021	0.097	*
β_{SL2}	-0.022	0.022	-0.069	0.020	
σ_{SP}	1.789	0.349	1.233	2.591	-
σ_{DE}	2.076	0.200	1.716	2.505	-

$\alpha 3$ is the intercept; β_{DBH}, the coefficient of diameter at breast height of a tree; β_{PG}, the coefficient of the number of pellet group within a plot; β_{SL2}, the coefficient of the slope of a plot; σ_{sp} and σ_{DE}, a vague uniform distribution from 0 to 100. If the 95% credible intervals of that estimated coefficient did not overlap 0, the factor was evaluated statistically significant. “-“ in "Significance" column indicates the meaninglessness of significance because σ_{SP} and σ_{DE} cannot take negative value.

Table S1 List of dominant species and their abundance in all plots

Species	*N*
Abelia spathulata Sieb. et Zucc.	1
Abies homolepis Sieb. et Zucc.	1
Abies mariesii Masters	1
Abies veitchii Lindley	3
Acer nipponicum Hara	2
Acer palmatum Thunb.	2
Acer pycnanthum K. Koch	6
Acer rufinerve Sieb. et Zucc.	5
Acer shirasawanum Koidz.	12
Akebia quinata (Thunb.) Decaisne	1
Alnus maximowiczii Call.	1
Artemisia japonica Thunb.	2
Artemisia princeps Pamp.	3
Aster glehni Fr. Schm. var. *hondoensis* Kitam.	1
Carpinus tschonoskii Maxim.	2
Corylus sieboldiana Bl.	3
Dryopteris classirhizoma Nakai	44
Enkianthus campanulatus (Miq.) Nicholson	27
Enkianthus perulatus (Miq.) Schneider	9
Fraxinus lauginosa f. *serrata*	14
Fraxinus mandshurica Rupr. var. *japonica* Maxim.	1
Hydrangea hirta (Thunb.ex_Murray) Sieb. et Zucc.	3
Hydrangea paniculata Sieb. et Zucc.	1
Kalopanax pictus (Thunb.) Nakai	2
Ligularia dentana (A.Gray) Hara	3
Ligustrum tschonoskii Dence.	16
Lonicera demissa Rehder	5
Lonicera gracilipes Miq.	4
Lonicera gracilipes var. *glabra*	65

Table S1 continued

Species	*N*
Oxalis corniculata L.	14
Pourthiaea villosa (Thunb.) Dence. var. *laevis* (Thunb.) Stapf.	3
Pterostyrax hispida Sieb. et Zucc.	4
Quercus crispula Blume	1
Reynoutria japonica Houtt.	1
Rhododendron japonicum (A.Gray) Suringar	10
Rhus ambigua Lavall. ex Dipp.	1
Rubus mesogaeus Focke	1
Rubus microphyllus L. fil.	4
Rubus palmatus Thunb. var. *coptophyllus* A. Gray	12
Rubus parvifolius L.	3
Sasa nipponica Makino et Shibata	1367
Sasamorpha borealis (Hack.) Nakai	132
Smilax sebeana Miq.	1
Spiraea cantoniensis Lour.	1
Swida controversa (Hemsl.) Sojak	7
Tsuga diversifolia (Maxim.) Masters	16
Tsuga sieboldii Carrière	3
Ulmus davidiana Planch. var. *japonica* (Rehder) Nakai	1
Viburnum dilatatum Thunb. ex Murray	1
Wisteria brachybotrys Sieb. et Zucc.	2
Unidentified species	230
No vegetation	15

Table S2 List of occurring tree species and their abundance in all plots

Species	*N*
Abies homolepis Sieb. et Zucc.	15
Abies veitchii Lindley	175
Acanthopanax sciadophylloides Franch. et Savat.	1
Acer carpinifolium Sieb. et Zucc.	2
Acer mono Maxim. var. *marmoratum* (Nichols.) Hara f. *dissectum* (Wesmael) Rehder	1
Acer mono var. *ambiguum*	10
Acer rufinerve Sieb. et Zucc.	3
Acer shirasawanum Koidz.	18
Acer sieboldianum Miq.	1
Acer tschonoskii Maxim.	2
Alnus hirsuta Turcz.	2
Alnus hirsuta Turcz. var. *sibirica* (Fischer) C. K. Schn.	14
Alnus matsuurae Call.	24
Alnus maximowiczii Call.	11
Benthamidia japonica (Sieb. et Zucc.) Hara	3
Betula corylifolia Regel et Maxim.	1
Betula davurica Pall.	47
Betula ermanii Cham.	77
Betula platyphylla Sukatchev var. *japonica* (Miq.) Hara	53
Carpinus cordata Bl.	4
Carpinus japonica Bl.	3
Carpinus tschonoskii Maxim.	23
Castanea crenata Sieb. et Zucc.	36
Chamaecyparis obtusa (Sieb. et Zucc.) Endl.	2
Chamaecyparis pisifera (Sieb. et Zucc.) Ebdl.	1
Clethra barvinervis Sieb. et Zucc.	90
Corylus heterophylla Fischer ex Basser var. *thubergii* Bl.	1
Corylus sieboldiana Bl.	6
Cryptomeria japonica (L.fil.) D. Don	1

Table S2 continued

Species	*N*
Enkianthus campanulatus (Miq.) Nicholson	29
Enkianthus sikokianus (Palibin) Ohwi	1
Euonymus alatus f. *striatus* (Thunb.) Makino	1
Fraxinus apertisquamifera Hara	2
Fraxinus lauginosa f. *serrata*	51
Fraxinus mandshurica Rupr. var. *japonica* Maxim.	2
Hydrangea paniculata Sieb. et Zucc.	8
Ilex macropoda Miq.	8
Kalopanax pictus (Thunb.) Nakai	6
Larix kaempferi (Lamb.) Carrière	572
Ligustrum tschonoskii Dencne.	6
Lindera sericea (Sieb. et Zucc.) Blume	1
Lindera umbellata Thunb.	9
Lonicera gracilipes var. *gladra*	2
Magnolia obovata Thunb.	1
Malus toringo (Sieb.) Sieb. ex Vriese	72
Meliosma myriantha Sieb. et Zucc.	1
Morus australis Poir.	4
Pinus densiflora Sieb. et Zucc.	55
Pourthiaea villosa (Thunb.) Dence. var. *laevis* (Thunb.) Stapf.	13
Prunus grayana Maxim.	3
Prunus maximowiczii Ruprecht	84
Quercus acutissima Carruthers	1
Quercus crispula Blume	355
Rhamnus davurica Pallas var. *nipponica* Makino	4
Rhododendron japonicum (A.Gray) Suringar	6
Salix bakko Kimura	1
Salix sachalinensis Fr. Schm.	1
Sorbus alnifolia (Sieb.et Zucc.) C. Koch	4

Table S2 continued

Species	*N*
Sorbus commixta Hedl.	8
Spiraea salicifolia L.	2
Swida controversa (Hemsl.) Sojak	18
Symplocos chinensis (Lour.) Druce var. *leucocarpa* (Nakai) Ohwi f. *pilosa* (Nakai) Ohwi	14
Tripterygium regelii Sprague et Takeda	1
Tsuga diversifolia (Maxim.) Masters	91

3. Contrasting effect of artificial grasslands on the intensity of deer browsing and debarking in forests

3.1 Introduction

Large ungulates (e.g., deer) are defined as a keystone species for ecosystem because they affect the distribution or abundance of several other species, and they change community structure by affecting the abundance of species at multiple trophic levels (Waller and Alverson 1997; Rooney 2001; Côté et al. 2004). The impact of large ungulates is generally negative for plant species diversity because deer intensively browse or debark palatable species (e.g., Rooney 2009; Iijima and Otsu 2018) that leads to the predominance of unpalatable plant species and the inhibition of recruitment of other species for decades (Royo et al. 2010; Tanentzap et al. 2012; Nuttle et al. 2014). However, some studies have shown that deer contribute to seed dispersal by excreting their pellets (Gill and Beardall 2001) and weaken the competition among plant species that increase the plant species diversity (Murray et al. 2016; Nishizawa et al. 2016). The intensity of deer impact on forest vegetation is known to be affected by deer density (Verheyden et al. 2006; Kiffner et al. 2008; Iijima and Nagaike 2015a). However, other factors such as light condition (Suzuki and Ito 2014; Iijima and Nagaike 2015a) and landscape components (Alverson et al. 1988; Moore et al. 1999) also affect the intensity of deer impact on forest vegetation (Fuller and Gill 2001).

The effect of landscape components on the intensity of deer impact on forest vegetation should be clarified (Putman 1996) because there are several landscape types even in natural ecosystems (e.g., evergreen forest, deciduous forest, and wetland) and human activities such as clear-cutting of forests, settlement of grasslands for cattle, and urbanization create a variety of landscapes. Previous studies have examined the effects of clear-cutting (Royo et al. 2017), the length of forest edge (Alverson et al. 1988; Vospernik 2006), agricultural land (Takada et al. 2002; Honda 2009), and artificial grasslands (Iijima and Nagaike 2017) on the intensity of deer impact on forest vegetation. Among these landscape components, artificial grasslands with abundant grasses are expected to affect food habit of deer species.

In Japan, the sika deer (*Cervus nippon*) is the only indigenous deer species, and the abundance of sika deer has been increasing in recent years (Takatsuki 2009; Iijima et al. 2013). Sika deer enter artificial grasslands (Takatsuki 1986; Kamei et al. 2010) and primarily utilizes artificial grasslands, except during winter in the mosaic landscape of forests and artificial

grasslands (Tsukada 2012; Iijima 2018). The population growth rate (Iijima et al. 2013) and the carrying capacities (Iijima and Ueno 2016) of sika deer are high in areas with abundant artificial grasslands. Consequently, the occurrence probability of debarking becomes high and the sapling density becomes low in forests surrounded by artificial grasslands (Iijima and Nagaike 2017). However, no study has yet evaluated the effect of artificial grasslands on sika deer impact on forest vegetation by considering the effect of deer density simultaneously. Because deer density increases deer impact on forest vegetation and deer density is affected by landscape components, including artificial grasslands as stated above, the effect of artificial grasslands on deer impact on forest vegetation should be examined by considering deer density.

In addition to deer density, the type of vegetation index and the species composition of vegetation to evaluate deer impact itself are also important factors for determining the intensity of deer impact. The occurrence of debarking (Akashi and Nakashizuka 1999; Kiffner et al. 2008; Takeuchi et al. 2011; Iijima and Nagaike 2015b) and the coverage of understory vegetation (Kaji et al. 2004; Nuttle et al. 2014; Tamura and Yamane 2017) had been widely used as the vegetation index to evaluate deer impact. However, the response of such vegetation indices to deer differs by species composition. For example, deer preferentially browse palatable plants (Mysterud 2006) such as Trillium species (Rooney 2009) and grassland specialist forb (Iijima and Otsu 2018) that lead to the increase of coverage of unpalatable species (Horsley et al. 2003). Furthermore, it has sometimes been demonstrated that plants' reaction to browsing impact differs even in case of similar species; for example, one of the dwarf bamboo species *Sasa nipponica* has browsing-tolerant characteristic, so that the possibility toward diminishing is lower even in case of high deer density. However, other dwarf bamboo species (e.g., *Sasa palmata* and *Sasamorpha borealis*) are not tolerant to browsing, and thus, they will decline or completely diminish when deer browse these species (Akiyama et al. 1977; Takatsuki 1983; Yokoyama and Shibata 1998; Nomiya et al. 2003).

Therefore, I conducted this study to clarify the effect of presence/absence of artificial grasslands on deer impact on forest vegetation. To accomplish this objective, I compared the occurrence of debarking and the coverage of understory vegetation in two adjacent regions under similar deer density with and without artificial grasslands in Yamanashi Prefecture, central Japan.

3.2 Materials and methods

3.2.1 Research site

This study was conducted in Mizugaki and Yatsugatake regions of Hokuto City, Yamanashi Prefecture, central Japan (Fig. 3.1). These two regions are adjacent to each other. Sika deer are distributed in these regions, and the sika deer densities in Mizugaki and Yatsugatake regions were estimated at 52.6 ± 28.8 (mean and standard deviation) and 53.4 ± 14.0 deer/km2 in 2016, respectively. I established 20 plots (10 plots in Mizugaki and 10 plots in Yatsugatake) in August and September 2018. The shape of each plot was a rectangle of 10 m × 40 m. The distance between plots was more than 500 m. The nearest distance between the plots in Yatsugatake and Mizugaki regions was 9.6 km that was within the mean seasonal migration distance of sika deer (9.9 km, Takii et al. 2012), and sika deer in these regions are genetically exchanged (Yuasa et al. 2006). Hence, sika deer populations in both regions are not distinct. In both regions, the forests are deciduous broad-leaved forests, and the predominant canopy tree species is primarily *Quercus crispula* (Table 3.1). Stand characteristics, size structure of trees, and species composition of both regions are similar (see Results for details). However, these two regions have different landscapes. Yatsugatake region is characterized by the mosaic landscape of forests and artificial grasslands, and the percentage of artificial grassland area is 11.4%. In this region, it was showed that some artificial grasslands were used by sika deer frequently, and grass consumption by sika deer was estimated two-thirds of grass produced in a pasture has none-fenced (K. Takarabe, unpublished data). In contrast, Mizugaki region is characterized by forest landscape, and the percentage of artificial grassland area is 0.0%.

3.2.2 Data collection

In August and September 2018, I measured the diameter at breast height (DBH), species, and the occurrence of debarking and fraying (hereafter, I shall use the word “debarking” for both debarking and fraying) by sika deer of all trees that were more than 3 cm in DBH within each plot. I established five 1 m × 1 m quadrats in each plot by 9 m along the long axis (i.e., 40 m) of the plot. In each quadrat, I surveyed the coverage of understory vegetation and the maximum height of understory vegetation by vegetation type. I evaluated the coverage of understory vegetation by 5% unit visually. I categorized the understory vegetation type as *S. nipponica*, *S. borealis*, forbs, unpalatable forbs (in this study, I confirmed them as *Macleaya cordata*, *Cynanchum caudatum*, and *Ligularia dentata)*, graminoids, tree saplings, and other

vegetation (e.g., moss). Dwarf bamboo is known to be resistant to deer browsing (Takatsuki 1983; Ando et al. 2006; Iijima and Nagaike 2015a), and forbs are preferentially browsed than graminoids (Rooney 2009). However, I will show only the coverage of understory vegetation because the coverage and maximum height of understory vegetation strongly correlated, and the trend of estimated coefficient by a hierarchical Bayes model with the maximum height of understory vegetation were similar. Furthermore, I took a tree canopy photo by a digital camera (Coolpix 4500, Nikon Corporation, Tokyo, Japan) with a fisheye lens (FC-E8, Nikon Corporation, Tokyo, Japan) at 1.3 m from the soil surface to evaluate canopy openness in each quadrat. Canopy openness was calculated from a photo by CanopOn2 (http://takenaka-akio.org/etc/canopon2/). The calculated canopy openness of Mizugaki and Yatsugatake regions were 11.9 ± 2.3% (mean and standard deviation) and 11.9 ± 1.3%, respectively.

Deer density of a square cell with a side of 5 km unit in 2016 in Yamanashi Prefecture was estimated by the model of Iijima et al. (2013). The deer density in each plot was defined as those in a cell where the plot located.

3.2.3 Statistical analysis

I intended to examine the effect of artificial grasslands on forest vegetation by comparing the occurrence of debarking and the coverage of understory vegetation between Mizugaki region without artificial grasslands and Yatsugatake region with abundant artificial grasslands. However, the occurrence of debarking and the coverage of understory vegetation are known to be affected by other factors. I compared the size distribution of trees and species composition of trees by Wilcoxon signed rank test and principal component analysis (PCA). These tests were conducted by R (R Core Team 2018). Furthermore, I developed a hierarchical Bayes model to examine the effect of artificial grasslands on deer impact on forest vegetation.

The model for the occurrence of debarking was as follows:

$$\mathrm{DE}_i \sim \mathrm{Bernoulli}(pd_i)$$

$$pd_i = \frac{1}{1 + \exp\left(-(\alpha 1 + \beta_{\mathrm{DBH}} \times \mathrm{DBH}_i + \beta_{\mathrm{SP},i} + \beta_{\mathrm{DD}} \times \mathrm{DD}_p + \beta_{\mathrm{RE}} \times \mathrm{RE}_p + \varepsilon_p)\right)}$$

DE_i is the occurrence of debarking that takes 1 if an ith tree was debarked or takes 0 if the tree was not debarked, α1 is the intercept, β_{DBH} is the coefficient of diameter at breast height of an ith tree (DBH_i), $\beta_{\mathrm{SP},i}$ is the random effect of tree species of an ith tree, β_{DD} is the coefficient of deer density of a pth plot (DD_p), β_{RE} is the coefficient of the variable region that takes 1 if a pth plot

was in Yatsugatake region or takes 0 if a pth plot was in Mizugaki region (RE_p), and ε_p is the random effect of a pth plot where ith tree located. Prior distributions of α1, β_{DBH}, β_{DD}, and β_{RE} were normal, with a mean value of 0 and a variance of 1000. Prior distributions of β_{SP} and ε_p were normal, with a mean value of 0 and variances of σ_{SP}^2 and σ_{PL}^2, respectively. Prior distributions of σ_{SP} and σ_{PL} were vague uniform, ranging from 0 to 100. In the analysis of the occurrence of debarking of standing trees, I excluded tree species that numbered < 10 in all plots.

The model for the coverage of understory vegetation was as follows:

$$CUV_q \sim \text{Beta}(\alpha_q, \beta_q)$$

$$\alpha_q = \mu_q \times \varphi$$

$$\beta_q = (1 - \mu_q) \times \varphi$$

$$\mu_q = \frac{1}{1 + \exp\left(-\left(\alpha 2 + \beta_{CO} \times CO_q + \beta_{VT,q} + \beta_{DD2} \times DD_p + \beta_{RE2} \times RE_q + \varepsilon 2_p\right)\right)}$$

CUV_q is the proportion of coverage of understory vegetation of a qth quadrat (i.e., 0 is minimum and 1 is maximum coverage), α2 is the intercept, β_{CO} is the coefficient of canopy openness of a qth quadrat (CO_q), $\beta_{VT,q}$ is the random effect of vegetation type in a qth quadrat, β_{DD2} is the coefficient of deer density of a pth plot (DD_p), β_{RE2} is the coefficient of the variable region that takes 1 if a qth quadrat was in Yatsugatake region or takes 0 if a qth quadrat was in Mizugaki region (RE_q), and $\varepsilon 2_p$ is the random effect of a pth plot. Beta distribution can take values between 0 and 1 and the shape of beta distribution is determined by two parameters (usually denoted as α and β). The expected value of beta distribution (μ) is defined as $\alpha / (\alpha + \beta)$. I would like to examine the effects of factors that were explained as above on the expected value of coverage (i.e., μ). It is convenient to introduce a new parameter $\varphi = \alpha + \beta$ to parameterize α and β. By using φ, α can be expressed as $\mu \times \varphi$ and β can be expressed as $(1 - \mu) \times \varphi$. If the coverage was 0 or 1, I added the value 10^{-6} to 0 or subtracted the value 10^{-6} from 1, respectively. Prior distributions of α2, β_{CO}, β_{DD}, and β_{RE2} were normal, with a mean value of 0 and a variance of 1000. Prior distributions of β_{VT} and $\varepsilon 2_p$ were normal, with a mean value of 0 and variances of σ_{VT}^2 and σ_{PL2}^2. Prior distributions of σ_{VT} and σ_{PL2} were vague uniform, ranging from 0 to 100. Prior distribution of φ was vague uniform, ranging from 0 to 1000. In the analysis of the coverage of understory vegetation, I excluded the vegetation type of *S. borealis* and unpalatable forbs because of a very small sample size.

Estimation of the posterior distribution of the hierarchical Bayes model was conducted by the Markov chain Monte Carlo (MCMC) method that was implemented by R (R Core Team 2018), JAGS (Plummer 2003), and the package "rjags" (Plummer 2018) of R (R Core Team 2018).

I ran three parallel MCMC chains and retained 10 000 iterations after an initial burn-in of 10 000 iterations. I thinned the sampled values to 10% (i.e., obtained 1000 samples as posterior distributions for each chain). MCMC sampling was considered to be converged when the "R hat" value became < 1.1 (Gelman et al. 2004). A coefficient was confirmed to be significantly affected (in terms of the response variable) if the 95% credible intervals of that estimated coefficient did not overlap 0.

3.3 Results

3.3.1 Stand characteristics

Tree densities of plots in Mizugaki and Yatsugatake regions were 1738 ± 835 (/ha, mean ± standard deviation) and 1530 ± 567 (/ha), respectively. Sum of tree basal area (BA) of plots in Mizugaki and Yatsugatake regions were 36.3 ± 7.4 (m2/ha, mean ± standard deviation) and 30.1 ± 5.4 (m2/ha), respectively. Size structures of trees of plots in both regions showed a typical L-shaped distribution with abundant small trees (Fig. 3.2) and there was no statistically significant difference between Mizugaki and Yatsugatake regions (P = 0.865, Wilcoxon signed rank test). Although the cumulative proportion of variance with axes 1 and 2 of PCA is not high (64%), tree species composition in the plots was primarily characterized by *Q. crispula*, *Fraxinus lanuginosa*, *Clethra barvinervis*, *Sorbus alnifolia*, and *Ilex macropoda*, and there was no obvious difference in tree species composition in Mizugaki and Yatsugatake regions because the PCA scores of plots in both regions mixed (Fig. 3.3). Therefore, the stand characteristics in both regions were similar.

3.3.2 Occurrence of debarking

The occurrence probability of debarking was significantly higher in Yatsugatake region than in Mizugaki region (Table 3.2). Deer density and DBH of each tree did not affect the occurrence probability of debarking (Table 3.2). The occurrence probability of debarking differed among tree species. *Stewartia pseudo-camelia*, *Swida controversa*, *C. barbinervis*, *F. lanuginosa*, and *I. macropoda* were significantly preferred, whereas *Betula platyphylla*, *Betula davurica*, *Betula ermanii*, and *Q. crispula* were significantly avoided (Fig. 3.4).

3.3.3 Coverage of understory vegetation

The coverage of understory vegetation was significantly higher in Yatsugatake region than in Mizugaki region (Table 3.3). Deer density and canopy openness had little impact on the coverage of understory vegetation (Table 3.3).

3.4 Discussion

3.4.1 Effect of artificial grasslands on deer impact on forests

Landscape components may modify the impact of white-tailed deer on vegetation (DeCalesta and Stout 1997). My study showed that artificial grasslands modified the deer impact on forest vegetation and that the effect of artificial grasslands completely differed with the occurrence of debarking (Table 3.2) and the coverage of understory vegetation (Table 3.3). Although tree size, tree species, and deer density per plot that were known to affect the intensity of tree debarking (Iijima and Nagaike 2015a) in addition to each plot-specific variation were considered in the analysis of the occurrence of debarking, the occurrence probability of debarking in Yatsugatake region with abundant artificial grasslands was significantly higher than that in Mizugaki region without artificial grasslands (Table 3.2). A previous study showed that the occurrence of debarking increased with a decrease in the distance from artificial grasslands (Iijima and Nagaike 2017). In contrast to the occurrence of debarking, the coverage of understory vegetation in Yatsugatake region was higher than that in Mizugaki region (Table 3.3). It has also been demonstrated that forest disturbances such as timber harvest increased forage production for wildlife (Greenberg et al. 2011), and browsing impact on forest vegetation weakened and ultimately disappeared as the proportion of forage-rich habitats (e.g., recent harvests) increased in landscape (Royo et al. 2017). Takada et al. (2002) found that plant species richness and plant coverage were significantly higher in forests adjacent to agricultural lands than in forests far away from agricultural lands; the authors also demonstrated that this difference was caused by the lower intensity of browsing in forests adjacent to agricultural lands due to the higher use of agricultural lands by the sika deer at these sites. The existence of perennial forage habitats increased the coverage of understory vegetation (Hurley et al. 2012). Thus, there are contrasting effects of alternative food sources (artificial grasslands in this study) on deer impact on forest vegetation in previous studies.

Gerhardt et al. (2013) hypothesized that red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and fallow deer (*Dama dama*) impact will increase in forests surrounded by food-rich habitats because when deer are disturbed during food intake in food-rich habitats, deer move and stay inside the surrounding forests and they will also engage in browsing or bark stripping activity to satisfy their energy demand. However, the results of my study showed that the occurrence of debarking was higher in forests adjacent to artificial grasslands, but the impact of browsing on understory vegetation was lower in forests adjacent to artificial grasslands. Thus, the hypothesis of Gerhardt et al. (2013) cannot explain the results. Food digestion characteristic of sika deer may explain the difference in deer impact on understory vegetation with the occurrence of debarking and the coverage of understory vegetation. Faber (1996) and
Ando et al. (2006) suggested that feeding high-quality forage such as grain to ruminants causes excess drop in pH in rumen fluid and prevents proper rumen function of moose and sika deer; therefore, deer feed on the bark to prevent bloating or lactic acidosis from upsetting rumen function. Then, 1) deer preferably forage high-quality grass in the grasslands, so that 2) deer forage less underground vegetation with relatively low-quality than grass, and 3) foraging high-quality food requires deer to forage bark for the rumen function. This relationship may depend on the balance of deer density and grassland area. My results support this hypothesis. To my best knowledge, this is the first study to demonstrate that the modification of deer impact on forest vegetation by landscape components showed a contrasting trend depending on vegetation index (tree debarking or the coverage of understory vegetation), although there are some studies that have demonstrated the effect of landscape on deer impact on forest vegetation for certain types of vegetation (Alverson et al. 1988; Takada et al. 2002; Royo et al. 2017）.

3.4.2 Effects of other factors on deer impact on forests

In addition to landscape components, deer impact on forest vegetation is affected by vegetation itself. The occurrence probability of debarking varied significantly among tree species (Fig. 3.4). Milligan and Koricheva (2013) indicated that browsing impact on saplings varied according to the combination of planted tree species. Although this effect was not considered in this study, if the selectivity of debarking is significantly different based on the combination of tree species, vegetation composition is also expected to strongly affect the intensity of debarking. Although the 95% credible intervals of all vegetation types about their coverage did overlap 0, the mean of posterior distribution of *S. nipponica* was higher than those of other vegetation types.

S. nipponica is a species resistant to browsing by sika deer (Takatsuki 1983; Ando et al. 2006; Iijima and Nagaike 2015a). Hence, even if deer density and landscape composition surrounding the forests are similar, the occurrence of debarking and the coverage of understory vegetation possibly varies according to the component of forest vegetation. The evaluation of deer impact on forest vegetation affected by landscape factor with vegetation index should be conducted carefully by considering not only landscape factor but also vegetation index and species composition.

Meanwhile, deer density had no significant impact on the intensity of debarking and the coverage of understory vegetation (Tables 3.2 and 3.3), although a high deer density causes an increase in the intensity of debarking (Kiffner et al. 2008; Iijima and Nagaike 2015a) and a decrease in the coverage of understory vegetation (Kaji et al. 2004; Nuttle et al. 2014; Tamura and Yamane 2017). Jarnemo et al. (2014) showed that the intensity of debarking correlated with deer density of red deer on the stand scale, whereas it was significantly affected by alternative forage abundance and landscape factor surrounding the forest rather than by deer density on the landscape scale. However, it should be noted that deer population dynamics are also affected by landscape components. The population growth rate (Iijima et al. 2013) and the carrying capacity of sika deer (Iijima and Ueno 2016) increase in areas with abundant artificial grasslands. Therefore, the effect of landscape components on deer impact on forest vegetation should be evaluated by considering deer density (Royo et al. 2017).

3.5 Figures

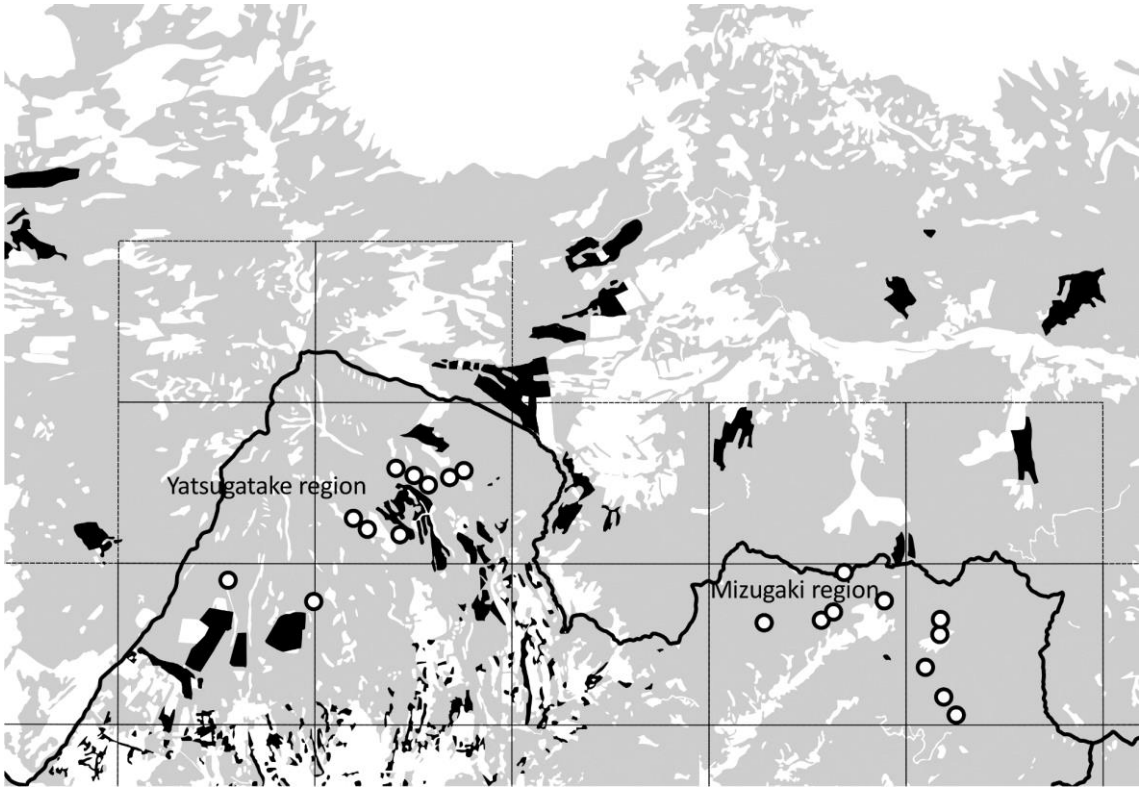

Fig. 3.1. Map of research site. Black and gray polygons indicate artificial grasslands and forests, respectively.

Solid lines are the boundary of Yamanashi Prefecture. Dotted lines are the grid cell of wildlife management unit of Yamanashi Prefecture. Empty circles are the location of my plots.

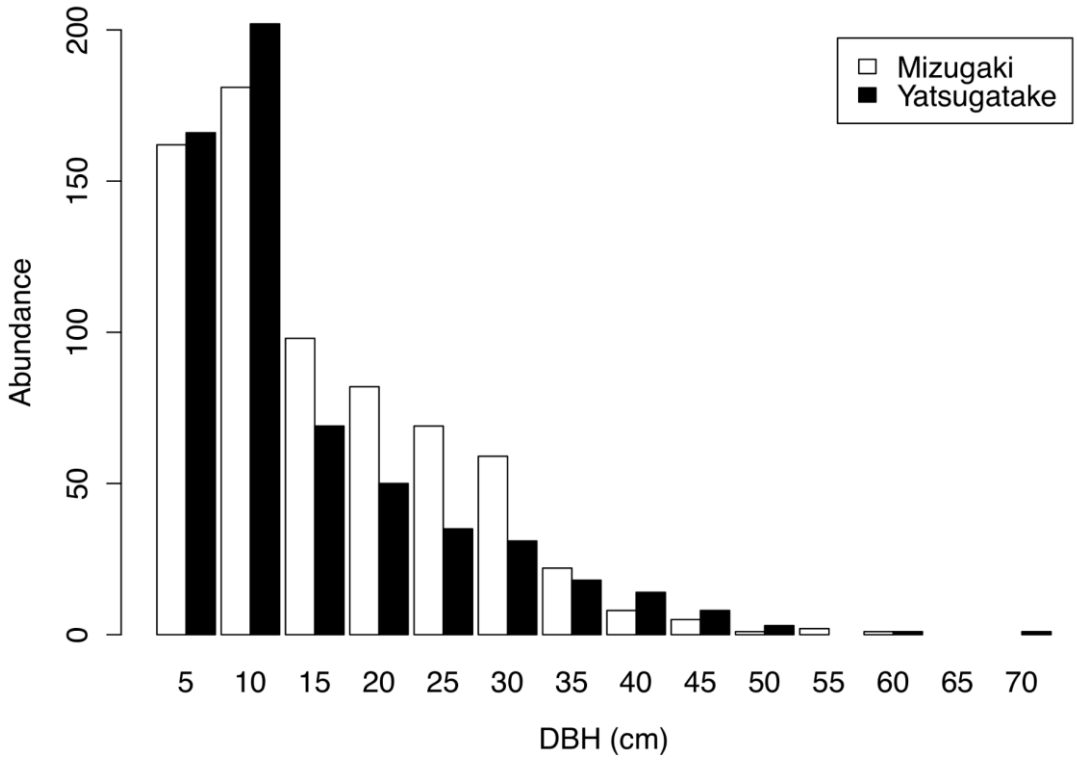

Fig. 3.2. Tree size structure of forests of plots in Mizugaki and Yatsugatake regions.

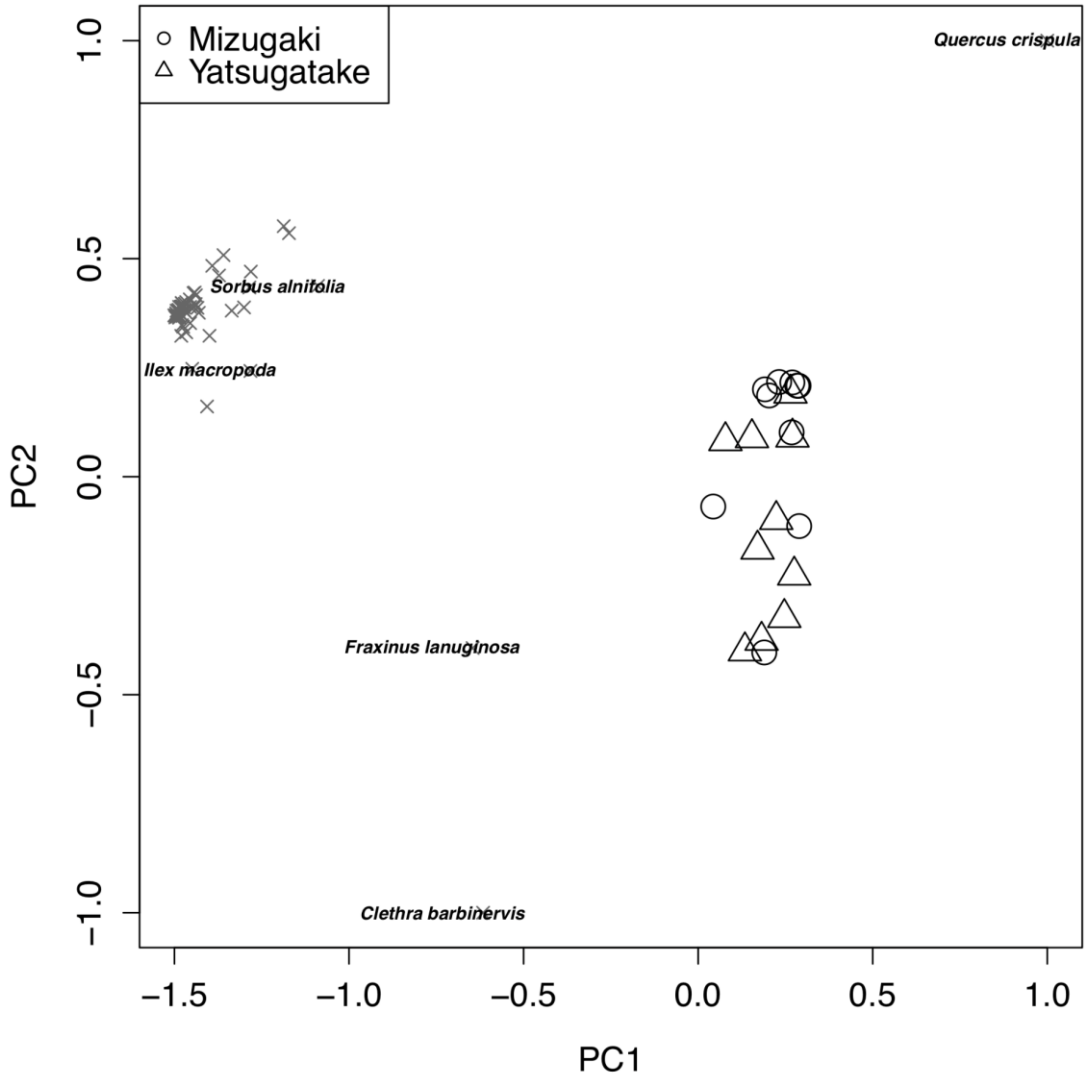

Fig. 3.3. Tree species composition of surveyed plots in Mizugaki and Yatsugatake regions that was evaluated by principal component analysis (PCA).

Empty circles and triangles indicate the PCA scores of plots in Mizugaki and Yatsugatake regions, respectively. Gray crosses indicate the CA scores of species. The Latin names of species were the top five species in tree density.

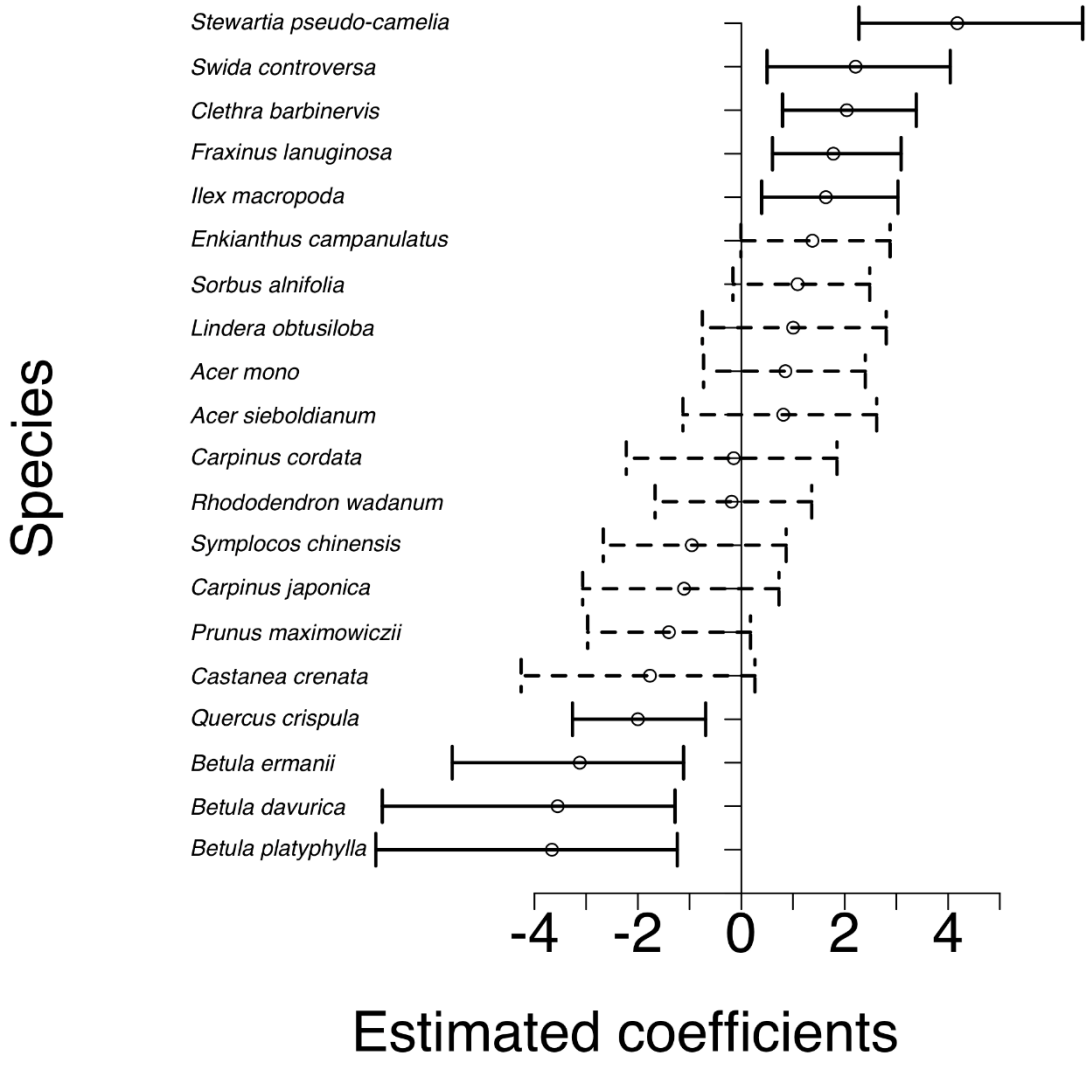

Fig. 3.4. The mean and 95% credible interval of estimated tree coefficient for the occurrence of debarking.

Solid and dotted lines indicate the 95% credible interval of coefficient did not overlap 0 (statistically significant effect on response variable) and overlapped 0, respectively.

3.6 Tables

Table 3.1 Stand characteristics of plots in Mizugaki and Yatsugatake regions

ID	Region	Tree density (/ha)	Basal area (m^2/ha)	Dominant species	
				Tree density	Basal area
p001	Mizugaki	1475	42.4	*Betula platyphylla*	*Betula platyphylla*
p002	Mizugaki	900	32.2	*Quercus crispula*	*Quercus crispula*
p003	Mizugaki	1175	33.4	*Quercus crispula*	*Quercus crispula*
p004	Mizugaki	3625	37.8	*Quercus crispula*	*Quercus crispula*
p005	Yatsugatake	1825	21.3	*Fraxinus lanuginosa*	*Quercus crispula*
p006	Yatsugatake	2100	31.8	*Fraxinus lanuginosa*	*Betula ermanii*
p007	Yatsugatake	1400	36.6	*Clethra barbinervis*	*Quercus crispula*
p008	Yatsugatake	1125	34.2	*Quercus crispula*	*Quercus crispula*
p009	Yatsugatake	1950	34.1	*Clethra barbinervis*	*Quercus crispula*
p010	Yatsugatake	2600	27.5	*Clethra barbinervis*	*Quercus crispula*
p011	Mizugaki	1175	27.6	*Betula davurica*	*Betula davurica*
p012	Mizugaki	2675	36.8	*Quercus crispula*	*Quercus crispula*
p013	Mizugaki	1475	47.0	*Quercus crispula*	*Quercus crispula*
p014	Mizugaki	1875	46.2	*Clethra barbinervis*	*Castanea crenata*
p015	Yatsugatake	1275	36.0	*Rhododendron wadanum*	*Quercus crispula*
p016	Yatsugatake	1175	24.8	*Clethra barbinervis*	*Quercus crispula*
p017	Yatsugatake	1100	24.0	*Quercus crispula*	*Quercus crispula*
p018	Yatsugatake	750	31.1	*Lindera obtusiloba*	*Zelkova serrata*
p019	Mizugaki	2000	33.4	*Sorbus alnifolia*	*Castanea crenata*
p020	Mizugaki	975	24.8	*Quercus crispula*	*Quercus crispula*

Table 3.2 Posterior summary of parameters of a hierarchical Bayes model for the occurrence of debarking

Coefficient	Mean	*SD*	95% credible interval		Significance
			Lower	Upper	
$\alpha 1$	–0.938	1.210	–3.144	1.579	
β_{DBH}	0.008	0.018	–0.027	0.042	
β_{DD}	–0.015	0.019	–0.051	0.021	
β_{RE}	1.355	0.645	0.123	2.627	*
σ_{SP}	2.392	0.563	1.559	3.717	-
σ_{PL}	1.341	0.295	0.883	2.021	-

A coefficient was confirmed to be significantly affected (in terms of the response variable) if the 95% credible intervals of that estimated coefficient did not overlap 0. "-" in "Significance" column indicates the meaningless of significance because σ_{SP} and σ_{PL} cannot take negative value.

Table 3.3 Posterior summary of parameters of a hierarchical Bayes model for the coverage of understory vegetation

Coefficient	Mean	*SD*	95% credible interval		Significance
			Lower	Upper	
$\alpha 2$	–2.540	0.440	–3.417	–1.710	*
β_{CO}	0.016	0.027	–0.036	0.071	
β_{DD2}	0.001	0.003	–0.005	0.008	
β_{RE2}	0.275	0.113	0.054	0.500	*
β_{VT}					
Forb	0.049	0.280	–0.473	0.627	
Graminoid	–0.212	0.283	–0.781	0.356	
Sasa nipponica	0.462	0.293	–0.065	1.063	
Others	–0.272	0.282	–0.844	0.285	
Tree saplings	0.048	0.282	–0.515	0.614	
φ	1.044	0.092	0.877	1.235	-
σ_{VT}	0.497	0.380	0.170	1.463	-
σ_{PL2}	0.058	0.045	0.002	0.169	-

A coefficient was confirmed to be significantly affected (in terms of the response variable) if the 95% credible intervals of that estimated coefficient did not overlap 0. "-" in "Significance" column indicates the meaningless of significance because φ, σVT, and σPL2 cannot take negative value.

5. General Discussion

5.1 Effects of artificial grasslands on deer impact on forest vegetation and future directions

Today, Japan is confronted with a declining and aging population. In particular, this social phenomenon is evident in hilly and mountainous areas, which has caused declines in agriculture, forestry, and farming and has increased the number of abandoned and/or denuded fields. Unmanaged fields become easier to use for sika deer, and therefore the influence of artificial landscapes on sika deer impact on forest ecosystems is expected to become stronger. Thus, it is very important to understand the processes by which artificial landscapes modify the impact of sika deer on forest vegetation, in order to seek a more effective way of maintaining the balance of forest ecosystems. My study established a starting point for generalizing the processes by which artificial grasslands modify the impact of sika deer on forest vegetation based on conclusive evidence.

Furthermore, my findings encourage the construction of deer-proof fences at boundaries between artificial grasslands and forests, to suppress artificial impacts on the dynamics of forest ecosystems. In Japan, deer population control has been conducted to decrease the damage on agricultural production and forest ecosystems. However, Takatsuki (2004) pointed out the object of sika deer management tends to mean reduction of deer population, not biodiversity conservation because 1) prefectural governments which conduct deer management tend to directly explain the degree of deer impact by deer population size and 2) most officers did not master ecology, so ecosystem management is often weak. Moreover, deer impact on forest vegetation is driven by deer density (Côté et al. 2004), individual species characteristics (Horsley et al. 2003), light conditions (Suzuki and Ito 2014), snow depth (Kiffner et al. 2008) and landscape surrounding forests. Therefore, population control does not necessarily suppress the deer impact on forest ecosystems. Excluding the artificial effects which prevent the normal function of forest dynamics is more important than deer population control, if the principle of natural regulation is respected in the conservation of natural ecosystems (Agetsuma 2013). Hester et al. (2000) also pointed out that large herbivores are an integral part of many forest ecosystems, meaning that their complete removal through fencing is considered undesirable in many natural forests. Hence, as an effective management, deer-proof fences should be constructed at boundaries between artificial grasslands and forests to suppress artificial effects on the dynamics of forest ecosystems, with careful consideration of forest ecosystems.

5.2 Sika deer feeding preferences

In Chapters 2 and 3, *Fraxinus lanuginosa*, *Clethra barbinervis*, *Swida controversa*, *Abies veitchii, Stewartia pseudo-camelia,* and *I. macropoda* were listed as significantly preferred by sika deer, whereas *Malus toringo, Betula platyphylla, Pinus densiflora, Betula davurica*, *Betula ermanii,* and *Q. crispula* were significantly avoided. Interestingly, deer feeding preferences differed quite a lot depending on area. For instance, *B. ermanii* is significantly debarked by sika deer in northwest Yatsugatake (which causes tree mortality), which is close to my study area (Tanaka et al. 2014). In addition, *I. macropoda* was significantly avoided by sika deer in Mt. Ohdaigahara (Kamata et al. 2008), *Q. crispula* was debarked in areas such as Kushiro Shitsugen National Park and Hokkaido (Inatomi et al. 2014). Takahashi and Kaji (2001) also demonstrated that deer food preference is very flexible and is quite dependent on region and habitat condition. In addition, the investigation at finer spatial scales showed that trees with small DBH were significantly more likely to be debarked by sika deer (Chapter 2), whereas the investigation at larger spatial scales showed that tree size did not affect the occurrence of debarking.

Ando et al. (2003) demonstrated that standing trees debarked by sika deer, including *F. lanuginose* and *C. barbinervis,* were not selected based on crude protein, fiber (hemicellulose, cellulose and lignin), or mineral content (Ca, Mg, Na, and K) in Mt. Ohdaigahara. Tamura and Ohara (2005) showed that there were no significant differences between debarked and none-debarked trees in terms of the amounts of chemical components including sugars, flavanols, polyphenols, and resins. Saint-Andrieux et al. (2009) also showed that beech bark was easier to peel off in summer than in autumn and winter, which are the sapless periods, correlating with debarking frequency. Moreover, bark composition was apparently similar in debarked and non-debarked trees, suggesting random selection of beech for bark consumption by red deer in summer (Saint-Andrieux et al. 2009). These previous studies focused on the chemical components and/or physiological reaction to debarking, which suggests that these may not be the key factors affecting deer feeding preferences. In addition, preferred tree species are quite different among areas, so further studies focusing on factors other than chemical components and physiological reaction are needed.

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